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Reef Fish Assemblages on Submerged Lava Flows of Three Different Ages[1]

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ABSTRACT: Recent volcanic activity near Kapa'ahu, Hawaii provided an opportunity to survey reef fish assemblages on submarine lava flows of three ages: 0.3 yr, 32 yr, and prehistoric. The results are used to examine development of these assemblages and influence of habitat characteristics on species distributions. Community-level analysis found clear differences between sites. Overall adult abundance and species richness increased with the age of the flow, but juvenile densities were highest on the youngest flow. Differences in abundances shown by many species may relate to habitat characteristics such as food availability, shelter, and conspecific densities.

IN DECEMBER 1986, lava from a continuing eruption of the Kilauea volcano on the island of Hawaii entered the ocean at Kapa'ahu. The underwater portion of the flow created an area of new substratum several hundred meters in width. This event presented a rare opportunity to study two different, but related, aspects of coral reef fish ecology.

The primary aim of the study is the description of the development of a coral reef fish assemblage in an area of new basaltic substratum. Community development on lava flows is a subject of considerable interest in the study of Hawaiian and Pacific natural history. Although terrestrial succession on lava is well studied, there are few studies of this process underwater.

Townsley and coworkers (1962) reported on colonization by algae, invertebrates, and fish of a large tidal pool created by the 1960 Kapoho eruption of Kilauea. Further studies were conducted by Doty (1972) of intertidal algal colonization. Grigg and Maragos (1974) described the development of coral communities on new lava substratum (see also Grigg 1983).

The development of a fish assemblage and its relationship to the development of the benthic community has never been followed on a submerged lava flow. Brock (1980) followed fish community development in an essentially similar situation at Honokohau Harbor on the Kona coast of the island of Hawaii for 11 yr after its creation. The harbor is an artificial embayment created by blasting from the existing coastline. The substratum consists of basaltic rock. Interpretation of the results of Brock's study was complicated, however, by the suboptimal nature of the habitat in the harbor. Consequently, it is difficult to extrapolate from these results to the development of Hawaiian fish communities in general.

A second aim of the study was to gain insight into the influence of certain habitat variables in producing the observed differences in abundance of various species in disturbed and adjacent undisturbed areas. Habitat characteristics shown to be important by other workers include food availability in the form of algal biomass (Kock 1982, Ogden and Ebersole 1981) and coral cover (Sutton 1985), availability of shelter (Shulman 1985), and presence and density of conspecifics (Sweatman 1983, Victor 1986) and competitors (Anderson et al. 1981, Hixon 1980). A third site at Kehena on Hawaii, where a 1955 flow entered the ocean, was included in the censuses both as a second reference area and as a midpoint in the chronology of community development between new and prehistoric.

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This paper is a report of the findings from a survey of the flow area in March 1987. The results are analyzed generally to describe differences between sites. Specific examples are used to evaluate the influences of food abundance, shelter, and conspecific density in producing the observed patterns.

MATERIALS AND METHODS

Three study sites on submerged lava flows of various ages (0.3 yr, 32 yr, and prehistoric) were selected along the southeastern coast of the island of Hawaii (Figure 1). All sites were exposed to the prevailing easterly tradewind-generated swell.

The study sites on and adjacent to the most recent lava flow were located at Kapa'ahu, Hawaii (19° N, 155° W). The November–December 1986 lava flow that entered the sea created an area of new shoreline approximately 300 m wide with small black-sand beaches at either side. The underwater portion of the flow was of similar width and extended to depths greater than 80 m.

The shoreline fronting the new flow consisted of sea cliffs 3 to 5 m high that continued vertically underwater to depths of between 5 and 8 m. High surge conditions as well as a visibility-limiting "mist" of fine air bubbles made surveying the shallow subtidal communities impossible. The deeper areas of the flow consisted largely of unconsolidated lava boulders, rocks, and rubble, with the bottom sloping into deep water at an angle of approximately 40 degrees (Figure 2).

The undisturbed area immediately to the

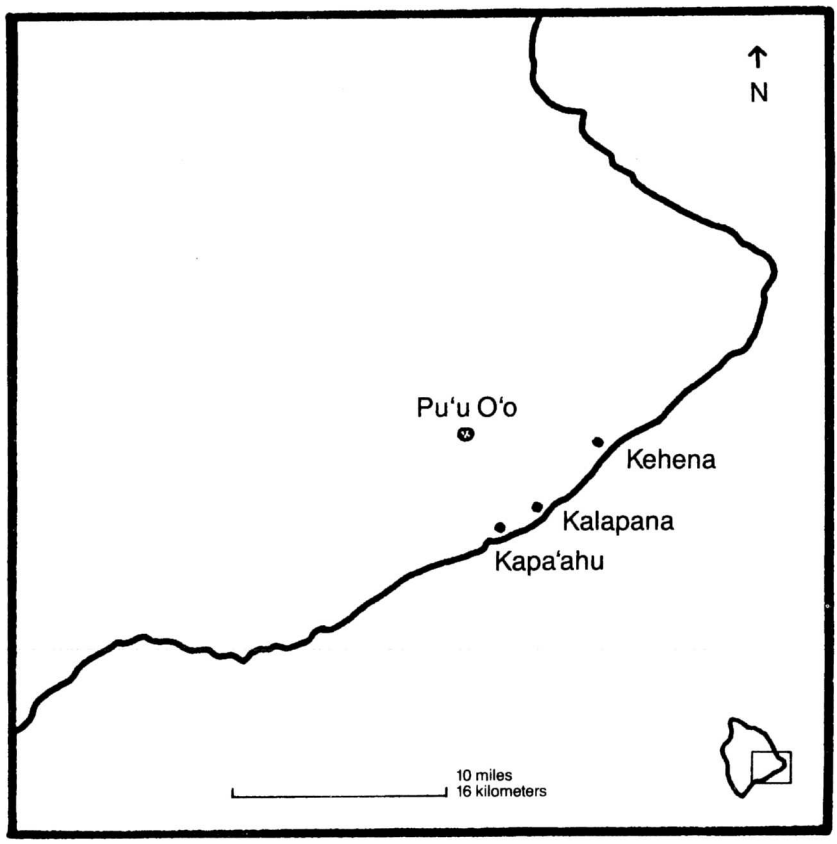

FIGURE 1. Map showing location of study sites. Inset depicts the island of Hawaii.

FIGURE 2. New flow, depth 8 m. Fish are *Chromis verater*.

northeast of the new flow was on a prehistoric flow of undetermined age. The substrate immediately offshore consisted of loose, wave-rounded lava rocks and sloped steeply to a depth of 8 m. Between 8 and 20 m the bottom sloped downward more gradually, and beyond the 20-m contour the bottom once again dropped away at a steep angle. The substratum between 8 and 15 m consisted of large (1–3 m diam.) boulders. *Pocillopora meandrina* was the most abundant coral, but cover was sparse (Figure 3). A well-developed coral community, dominated by *Porites compressa* and *Porites lobata*, was found between 15 and 20 m.

The study site at Kehena was located on the southwestern part of a 1955 a'a flow. Unlike the recent flow at Kapa'ahu, the 1955 flow extended to only moderate depths, reaching a black-sand bottom at 20 m. The flow itself consisted of rocks, rubble, and scattered boulders. The substratum was more stable than at the Kapa'ahu flow because of the growth of live coral (primarily species of *Porites* and *Montipora*) that cemented together much of the loose material.

The purpose of using the three sites described above was to provide a chronology of development of the assemblage of reef fishes. Originally, we had planned to follow the Kapa'ahu site over time. However, continuing inundation by new lava made this impossible. Examining a number of sites of different ages was felt to be the next best approach. This is the design employed by Grigg and Maragos (1974). Inclusion of the site at Kehena also allowed comparison of the Kapa'ahu sites with a third site. Hereafter, the new flow and adjacent undisturbed sites at Kapa'ahu are referred to as new and prehistoric, respectively. The Kehena site is referred to as the 32-yr site.

At each site, three replicate 30-m transect lines were laid along both the 9-m and 18-m

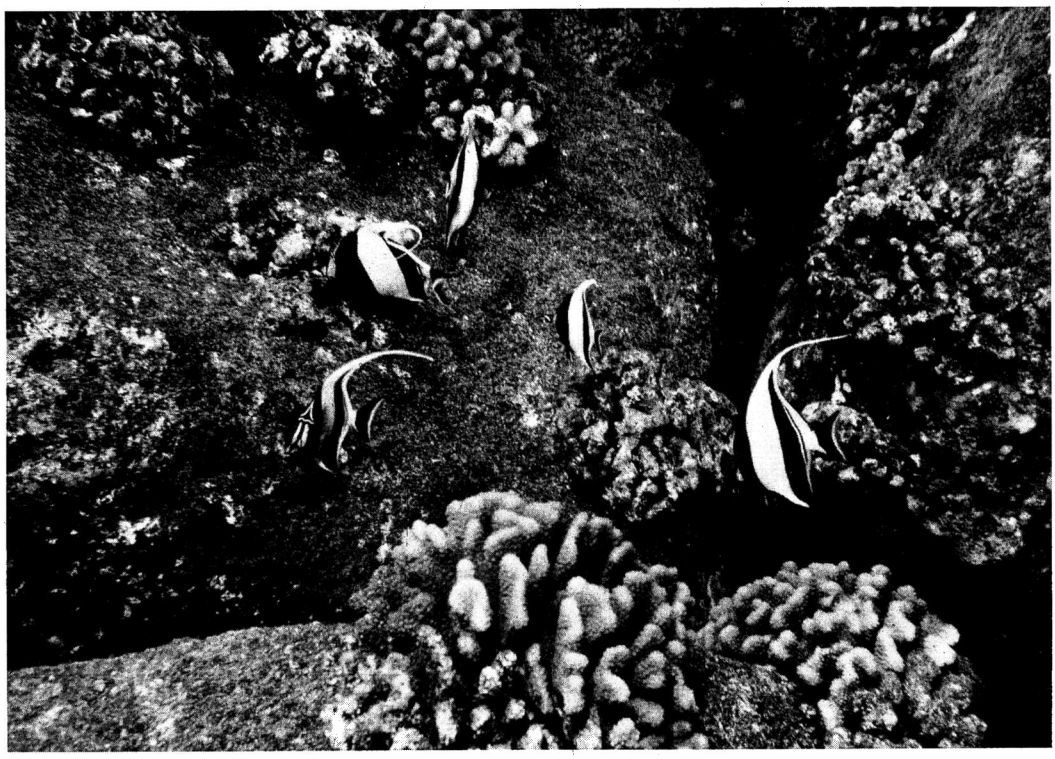

FIGURE 3. Prehistoric flow, depth 8 m. Fish are *Zanclus cornutus*; corals are *Pocillopora meandrina*.

depth contours, for a total of six transects per site. Each census was performed by a diver swimming the length of the line and recording the numbers of individuals of each species observed within 3 m of either side (Brock 1954). The total transect area was 180 m^2. Counts were made only once along a given transect. No systematic attempt was made in the transect counts to avoid a "scare" factor resulting from the laying of the transect line shortly before counts were made, as described by Fowler (1987).

For some of the species encountered, juveniles and adults were counted separately. This distinction was straightforward in most cases for two reasons. First, recruitment is strongly seasonal in most species of Hawaiian reef fishes, with a peak in the summer months (Walsh 1987). The surveys for this study were conducted at the very beginning of this recruitment season, and size differences between young-of-the-year and adults were extreme. Second, juveniles of many species show striking differences in color pattern from adults. The wrasse *Thallosoma duperrey* and the surgeonfish *Ctenochaetus hawaiiensis* are two such species.

All statistical analyses except the cluster analysis were performed either with the SAS system or by hand calculation. The Kruskal–Wallis nonparametric analysis of variance procedure was used in comparing species and family densities across sites because of heterogeneity of variance in several cases. Tukey-type multiple comparisons were used for pairwise comparisons of sites. These and the other procedures utilized are explained in detail by Zar (1984). Unless otherwise stated, significance levels are 0.05.

The cluster analysis was performed on an IBM 3081 mainframe computer. Briefly, the program generates a similarity matrix based on Motyka's modification of the Sorensen similarity coefficient (Mueller-Dombois and

Bridges 1981). Individual transects were used as the classification units and levels of linkage were determined using the unweighted paired-group clustering method (UPGMA). Higher levels of linkage indicate greater similarity between classification units (transects).

RESULTS

Cluster analysis of species counts from the six transects at each site was used to examine overall assemblage similarity between sites. The results of this analysis are illustrated in a dendrogram (Figure 4). Clear separation of the new site from both the prehistoric and 32-yr sites was evident. The two depths within the new site show close linkage (1–3: 9 m, 4–6: 18 m). The prehistoric and 32-yr sites were not separated clearly, although some adjacent transects within depths showed high levels of linkage (e.g., 7–9: prehistoric flow 9 m; 11–12: prehistoric flow 18 m; 14–15: 32-yr flow 9 m). This analysis indicated both that assemblages differed between depths within sites and that although the assemblage at the new site was very different from either of the older site assemblages, these older site assemblages were not substantially different from each other.

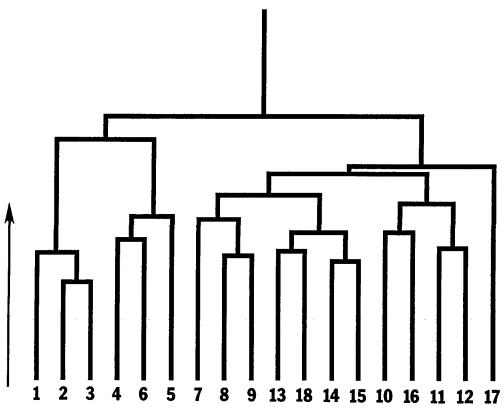

FIGURE 4. Dendrogram depicting results of cluster analysis of species counts. Arrow indicates direction of decreasing similarity. Transect numbers are shown along bottom (1–3: new flow, 9 m; 4–6: new flow, 18 m; 7–9: prehistoric, 9 m; 10–12: prehistoric, 18 m; 13–15: Kehena, 9 m; 16–18: Kehena, 18 m.

The mean numbers of species encountered in transect counts at the three sites were all significantly different from each other (Figure 5). Species richness increased with the age of the flow. If species numbers are taken as an indicator of assemblage diversity, this showed an increase in diversity with community age.

A similar trend was seen in mean adult density across the three sites, but only the new and prehistoric sites were significantly different (Figure 5). Juvenile density at the new site was significantly higher than at the 32-yr site, but not different from that at the prehistoric site.

The above analyses gave only information as to the similarity of the entire assemblages at each of the sites. To determine which groups contributed to these differences, it was necessary to examine family and species distributions individually.

Densities of the eight most common families were compared across sites (Table 1). Differences among sites were found for three families: acanthurids, chaetodontids, and zanclids. No between-site differences were found for the balistids, cirrhitids, labrids, mullids, or pomacentrids.

The mean densities for the 51 most common species at both depths for each of the three sites are shown in Table 2. Densities at each depth are shown separately to show differences in depth distributions within species, but depths were combined for statistical comparisons. Examples of species where density differences with depth were suggested include the pomacentrids *Chromis agilis* and *Chromis hanui*, the pomacanthid *Centropyge potteri*, and the mullid *Parupeneus multifasciatus* (Table 2).

Fourteen species showed density differences among sites; seven of these differences were significant at the 0.01 level (Table 2). The species showing differences mostly belong to the families mentioned above that showed differences between sites and will be discussed below.

The acanthurids (surgeonfishes), representing the bulk of the herbivore guild, showed a highly significant difference in density among sites ($H = 12.78$, $P < 0.001$). The prehistoric site had higher acanthurid densities than the new site, but did not differ from the 32-yr site

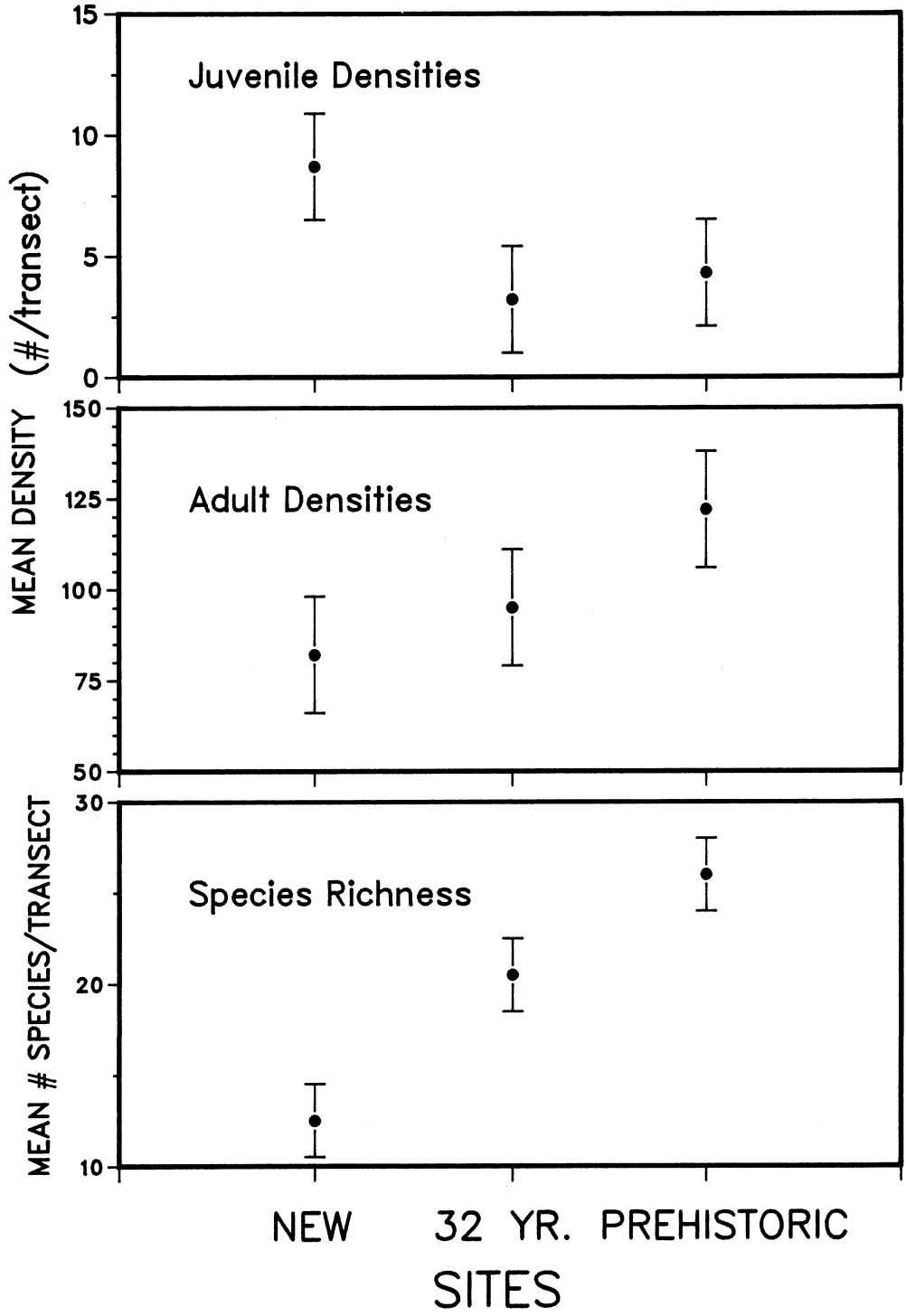

FIGURE 5. Comparison of juvenile densities, adult densities, and species richness for the three sites. Sampling size is six transects each of 180 m^2 at each site. Dots indicate means; vertical bars indicate least significant differences (if bars from two means do not overlap, they are significantly different at the 0.05 level).

TABLE 1

MEAN DENSITIES BY FAMILY AT THE THREE SITES[a]

FAMILY	COMMON NAME	MEAN DENSITY NEW FLOW	32-YR FLOW	PREHISTORIC FLOW	
Acanthuridae	Surgeonfishes	4.2	18.7	33.2	*
Balistidae	Triggerfishes	20.5	18.2	14.2	
Chaetodontidae	Butterflyfishes	1.7	7.7	8.0	*
Cirrhitidae	Hawkfishes	2.2	3.7	2.5	
Labridae	Wrasses	7.7	6.8	9.7	
Mullidae	Goatfishes	8.2	4.2	5.8	
Pomacentridae	Damselfishes	37.8	28.2	37.8	
Zanclidae	Moorish Idols	0	2.0	3.8	*

[a] Significant differences are indicated by asterisks (*, $P < 0.05$). Means connected by underlining are not significantly different.

($0.10 > P > 0.05$) in this respect. Acanthurid densities of the new and 32-yr sites were not different. Comparing densities of the two most common surgeonfish species, *Ctenochaetus strigosus* and *Zebrasoma flavescens*, gave similar results. New-site densities of both species were lower than those at either of the older sites (*Z. flavescens*: $H = 10.77$, $P < 0.01$; *C. strigosus*: $H = 10.96$, $P < 0.01$).

The chaetodontids (butterflyfishes) also showed significant differences in abundance between sites. Butterflyfish densities were lower at the new site than at either the prehistoric or 32-yr sites (overall: $H = 10.44$, $P < 0.01$). Densities at the two older sites were not different. Densities of the two most common butterflyfish species, *Chaetodon multicinctus* and *Chaetodon ornatissimus*, showed a similar pattern. *C. multicinctus* was less abundant at the new site than at either of the older sites ($H = 11.51$, $P < 0.001$). *C. ornatissimus* densities were lower at the new site than at the 32-yr site, but not different from those at the prehistoric site. These species are obligate coral feeders (Reese 1977).

The third family showing differences among sites was the Zanclidae. This family contains only the Moorish Idol, *Zanclus cornutus*. *Zanclus* densities were lower at the new site than at the older sites, while those at the older sites were not different ($H = 8.552$, $P < 0.01$).

Because of sampling error, the Kruskal–Wallis procedure will indicate a significant difference when none exists (a Type I error [Zar 1984]) 5% of the time at an alpha level of 0.05. The large number of comparisons made here (51) should therefore produce two to three such differences. Nonetheless, the trends identified appear to be robust.

Two other interesting distributional patterns were observed. The first was the apparent habitat separation of juveniles and adults seen in *Ctenochaetus hawaiiensis* and *Thallosoma duperrey*. In both species, more juveniles were counted on the new flow than in the prehistoric area (Table 2).

The second of these patterns was seen in the planktivorous damselfishes. The three small species (*Chromis agilis*, *Chromis hanui*, and *Chromis ovalis*) were not seen on the new flow, but were moderately abundant in the prehistoric area (Table 2). In contrast, *Chromis verater* was abundant on the new flow and absent both on the prehistoric and 32-yr flows.

DISCUSSION

Community Development

Species richness and total fish density increase with the age of the lava flow. After 3 months, the number of species on the recent

TABLE 2

MEAN DENSITIES OF THE 51 MOST ABUNDANT SPECIES AT THE THREE SITES[a]

SPECIES	SITE						
	NEW FLOW		32-YR FLOW		PREHISTORIC FLOW		
	9 m	18 m	9 m	18 m	9 m	18 m	
Acanthuridae							
Acanthurus achilles	0.33	—	2.33	1.33	4	—	
A. nigrofuscus	0.33	—	0.67	1.67	6.67	—	
A. nigroris	—	—	—	—	2	—	
A. olivaceus	—	0.33	—	2	—	2	
Ctenochaetus hawaiiensis	0.33	2.67	—	—	2.33	1.67	*
C. strigosus	—	—	4.67	6.67	16.67	7	**
Naso hexacanthus	—	2	—	—	1	1.33	
N. lituratus	—	—	0.67	0.33	0.67	1	*
Zebrasoma flavescens	1.33	0.67	6.33	10	10.67	7	**
Balistidae							
Melichthys niger	—	0.33	—	1	—	—	
Pervagor spilosoma	25	15.33	17.67	16.67	16.33	11	
Chaetodontidae							
Chaetodon multicinctus	—	—	3	4.33	3.67	2.67	**
C. ornatissimus	—	—	1.67	1.67	2	0.33	*
C. quadrimaculatus	1	—	0.33	0.67	1.33	—	
Forcipiger flavissimus	—	0.33	0.67	1.33	1.67	2.67	*
Cirrhitidae							
Cirrhitus fasciatus	1	—	—	0.33	—	—	
C. pinnulatus	1	—	—	—	—	0.33	
Paracirrhites arcatus	1.33	1	3	3.67	2	2.67	**
Holocentridae							
Myripristis amaenus	—	—	—	—	3.33	—	*
Labridae							
Gomphosus varius	—	—	—	1	—	—	
Labroides pthirophagus	0.33	—	0.67	0.33	0.33	1.67	
Thallosoma duperrey	11	3.33	4	4.67	10.67	3.67	
Lutjanidae							
Lutjanus kasmira	—	—	5	2.33	3.67	—	
Mullidae							
Mulloides vanicolensis	—	—	—	—	3	0.67	*
Parupeneus cyclostomus	1	0.67	—	—	0.33	0.67	
P. multifasciatus	5	9.33	1.67	6.33	2.67	4	
Pomacanthidae							
Centropyge potteri	—	—	—	1.33	—	4	
Pomacentridae							
Chromis agilis	—	—	—	2.67	—	7	
C. hanui	—	—	—	1.67	—	4.33	
C. ovalis	—	—	—	—	—	1.33	
C. vanderbilti	53.33	15	26.67	16.67	30.67	30	
C. verater	3	2.67	—	—	—	—	***
Plectroglyphidodon johnstonianus	0.33	—	1.33	2	1.66	—	*
Stegastes fasciolatus	1	—	3.33	2	0.67	—	**
Zanclidae							
Zanclus cornutus	—	—	1.67	2.33	3.67	4	**

[a] Significant differences are indicated by asterisks (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Means connected by underlining are not significantly different.

flow was approximately 50% that of the nearby area of prehistoric age. Brock (1980) reported similar results for fishes colonizing freshly exposed basaltic substratum at Honokohau Harbor. The number of species recorded at Honokohau was approximately 70% of the total number at a nearby undisturbed site after 1 yr. Species numbers continued to increase asymptotically, and a stable peak was reached by 5 yr. However, this peak number was lower than at the undisturbed reference site. This difference was attributed to the suboptimal nature of the habitat inside Honokohau Harbor. The number of species encountered at the 32-yr site in this study was significantly lower than that at the prehistoric site. The rapid initial increase in species numbers seen at Kapa'ahu is similar to Brock's findings but attainment of peak species numbers takes much longer at Kehena (5 yr at Honokohau versus more than 32).

This apparent disagreement with Brock's results has at least two possible causes. Both the 32-yr and prehistoric sites may have supported assemblages that were as mature as they would get and the difference in species richness was due to recruitment levels, benthic communities, or some other factor. Were this the case, the 32-yr site would not represent an intermediate stage between the new and prehistoric flows. Alternatively, peak species richness may be reached more rapidly in the unusual habitat of Honokohau Harbor than in a more typical Hawaiian habitat, making the findings there nonrepresentative. The development of the fish assemblage there might not be paced by coral development as would be expected elsewhere.

A different pattern was observed for assemblages of corals developing on lava flows on Hawaii by Grigg and Maragos (1974). Peak diversity is reached at an intermediate stage of development. Along the exposed southeastern coast of Hawaii, coral communities are kept in an intermediate, high-diversity stage of succession through continual exposure to strong ocean swells. This stage is reached in about 15 yr. On the sheltered western coast, succession proceeds to a low-diversity climax stage over a period of more than 50 yr.

The Intermediate Disturbance Hypothesis proposed by Connell (1978) predicts the type of community development observed for corals on Hawaii. The apparent difference between corals and fishes may be due simply to the nature of sampling performed. A fish community associated with a mature coral community was not examined in this study because it was performed on the exposed southeastern coast of Hawaii. In Brock's study, a mature coral community would not yet have developed at any of his sites. If diversity of fishes closely follows diversity of corals (and if coral diversity is indicative of benthic diversity in general), then the decrease after the intermediate stage may not yet have occurred at Honokohau. In both cases, the continual increase in species numbers would be expected.

Alternatively, the processes operating in coral and fish communities may be different. The decrease in diversity as the community matures in the Intermediate Disturbance model is due to displacement of opportunistic species by competitive dominants as competition for some resource intensifies. For corals this resource is space. There is little evidence to support or refute the model from communities of motile organisms where the limiting resource may be something other than space (Connell 1978).

Support for the existence of strong interspecific competition and competitive exclusion in reef fishes is scarce, but does exist (e.g., Hixon 1980). In Hawaii, where recruitment levels are generally low (Walsh 1987), populations may not typically be at carrying capacity, further reducing any role of interspecific competition in structuring assemblages. Sale and Douglas (1984) have suggested that reef fish assemblages may be maintained below carrying capacity by insufficient recruitment, with consequently high species diversity. Examination of fish assemblages associated with all stages of benthic community development will be necessary to determine: (1) how intimately related diversity change in a fish assemblage is related to change in the benthic community, and (2) whether reef fish assemblages exhibit the pattern predicted by the Intermediate Disturbance model.

Influence of Habitat Variables

Differences in the abundance of some species between new and older flow areas may be explicable by factors such as the availability of food, shelter, and density of conspecifics. These will be discussed below along with groups whose distributions appear to be strongly affected by each. With the exception of species that show higher abundances on the new flow, most of the patterns to be discussed could also be accounted for by a lack of adult migration into the disturbed area. Two observations suggest that some characteristic(s) of the substratum on the new flow influence species distributions and are worth examining. Sufficient migration of adults took place to make densities of five of the major families indistinguishable in the new and prehistoric flow areas. Second, the three families that showed differences between new and prehistoric flow areas were all substratum feeders.

The unstable substratum on the new flow appears to be a poor environment for survival of sessile organisms. The large rocks that composed much of the bottom appeared to shift and roll frequently. In a directly analogous situation, Sousa (1979) found that frequent rolling of the smallest rocks in an intertidal boulder field limited the development of an algal community on them. Inadequate food resources likely limited abundance of the three families observed to have lower densities on the new flow.

Lack of coral on the flow almost certainly accounts for the absence of adult coral-feeding chaetodontids such as *Chaetodon multicinctus* and *Chaetodon ornatissimus*. Both species are moderately abundant in the adjacent undisturbed area. Ideally, changes in the abundance of both these butterflyfish species and their coral prey should be monitored over a long period. We predict that a close correlation would be found, as suggested by Reese (1981) and Hourigan et al. (1988).

Acanthurid and zanclid densities may also be limited by scarce food resources. Both are dependent on a benthic food base that takes time to develop (algae for surgeonfish; algae, sponges, and tunicates for Moorish Idols [Randall 1985]) and is probably susceptible to the frequent disturbances on the new flow. Algal biomass was not measured, but no notable algal growth was observed. The lack of even filamentous species despite the relative lack of herbivores is suggestive of the frequency of disturbance. In contrast, Brock (1980) found that three of the most abundant fish colonizing Honokohau Harbor were acanthurids. However, the period preceding the first census was longer (approximately 1 yr) and the protected nature of the harbor probably prevented disruption of benthic community development. Kock (1982) found that herbivorous damselfishes did not colonize a sunken barge in Guam until an algal mat had developed.

If available food resources account for the distributional patterns discussed above, the rate and latency of colonization by groups dependent on different resources should reflect the time course of development of those resources. After 1 yr, a large tide pool created by the 1960 Kapoho eruption on Hawaii had a thriving community of algae and various invertebrates but no notable coral growth (Townsley et al. 1962). A similar pattern of benthic development would be expected on the larger scale examined here. The prediction that follows is that densities of acanthurids and Moorish Idols on the new flow will approach those of the adjacent undisturbed area more quickly than will densities of coral-feeding butterflyfishes.

Suitable shelter may also be a limiting resource on the new flow. Shulman (1985) found that recruitment to artificial reefs increased when the amount of shelter offered by the reef was enhanced. The lower abundances or absence of several species of small planktivorous damselfishes on the flow, for whom food should not be limiting, suggest that some sort of substrate complexity or heterogeneity may be lacking. Presumably, abundant shelter is important for small fishes exposed to predators while feeding in the water column. Availability of cover could also explain the site differences discussed above for acanthurids and zanclids.

Intraspecific and Intrafamilial Distributional Patterns

The apparent juvenile-adult differences in *Ctenochaetus hawaiiensis* and *Thallosoma duperrey* are intriguing. We do not feel these are sampling artifacts because both species have juvenile color patterns that differ strikingly from those of adults and the juveniles are visible and active, making them easy to census. Assuming the patterns are real, several causes for their occurrence are possible.

The inversely related distributions could be produced by differential settlement or survival of juveniles in the two areas. Active avoidance of adults after settlement would give rise to this pattern. Our data do not allow separation of these alternatives.

Habitat segregation between adults and juveniles has been documented for five species of Indian Ocean surgeonfishes (Robertson et al. 1979). These workers suggested that differential habitat use reduced intraspecific competition and adult aggression directed toward juveniles. Evidence exists for intraspecific competition in *Thallosoma bifasciatum*, a Caribbean congener of *Thallosoma duperrey*. Victor (1986) demonstrated lowered juvenile growth rates with increasing adult density in *T. bifasciatum*. The juvenile color patterns exhibited by both *Ctenochaetus hawaiiensis* and *T. duperrey* may also represent adaptations to reduce competition or aggression from adults as shown by Fricke (1980) for the angelfish *Pomacanthus imperator*.

The distributional patterns seen in the planktivorous damselfishes were particularly interesting. The three species present in the prehistoric flow area but absent on the new flow (*Chromis agilis*, *Chromis hanui*, and *Chromis ovalis*) are common in most of Hawaii in shallow water. In contrast, *Chromis verater* is typically only seen in deeper water, where it is often the dominant species (Randall 1985). The absence of the former three *Chromis* species in the new flow area may provide a competitive release and allow an upward range extension in *C. verater*. Hixon (1980) demonstrated that vertical habitat segregation in two species of California surfperch of the genus *Embiotoca* was the result of competitive interactions. *Embiotoca jacksoni* was restricted to deeper water by the aggressive dominance of *Embiotoca lateralis*. Removal of *E. lateralis* allowed *E. jacksoni* to move into and forage on the substratum in shallow areas. Competition for planktonic food resources, but not habitat segregation, has been shown in a reproductive study of the damselfish *Acanthochromis polyacanthus* (Thresher 1983).

Other possibilities that may account for the observed distribution of the planktivorous damselfishes are a lack of normal predators and the particular substratum characteristics of the new flow. A difference in predator density seems unlikely to be responsible as it is difficult to account both for the absence of the three normal shallow-water *Chromis* species and the presence of *Chromis verater*. Lack of cover may also prevent the shallow-water *Chromis* from colonizing the new flow (note that these species were also absent at the 9-m depth contour on the prehistoric flow, which appeared to offer less cover than the deeper area), but the cover requirements of *C. verater* may be less stringent. This would not account for the absence of this species in the prehistoric flow area, however. Experiments such as those performed by Hixon (1980) are necessary to differentiate between these possibilities.

Reef fish community development has been documented broadly here by surveying sites of different ages. There are problems with this approach. The important events in this development are likely concentrated in the short period after initial disturbance. The Kapa'ahu flow was censused at only one point, 3 months, with a gap of 30 yr until the next measured stage in community change. The continuing nature of the eruption and covering of the study site by new flows have made a sequence of visits impossible. Interpretation is also complicated by the possible differences in the histories of the sites used here (e.g., storms), local oceanographic conditions, and demographic processes such as stochastic differences in recruitment.

Three months after the flow of lava into

the sea had ceased, disturbance due to the unstable nature of the substrate was probably still the primary factor influencing fish community structure. The normal factors influencing community structure, such as competitive interactions and recruitment processes, are probably overshadowed by this continuing disruption. Long-term monitoring of a single site after the current eruption ceases will be necessary to fully describe development of the fish assemblage.

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